National Park Service
Channel Islands National Park

**Status and Trend of Island Fox,
San Miguel Island,
Channel Islands National Park**

Technical Report 98-01

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ACKNOWLEDGMENTS

ABSTRACT

Island foxes (*Urocyon littoralis littoralis*) were monitored on 3 grids on San Miguel Island, California, from 1993 to 1997. Capture-mark-recapture techniques were used to estimate adult fox densities annually on the 3 grids. An abrupt decline in the island fox population on San Miguel Island, California, was observed during the study period. On 1 grid, fox density declined from a high of approximately 15 adult fox/km^2 to less than 1 fox/km^2. The decline occurred first on the west side of the island, and subsequently on the east side. The observed declines were not accompanied by declines in food availability, at least as measured by density of deer mice (*Peromyscus maniculatus*) or cover of sea-fig (*Carprobrotus chilensis*), two important food items. We did not monitor annual variation in insect abundance, which may have affected fox populations. The observed population decline was not correlated with changes in winter precipitation.

A serological survey suggested that canine disease was not a factor in the observed decline, although without clinical evidence of disease from carcasses and documented mortality, the influence of disease cannot be confirmed or refuted. Fox blood samples were collected in 1994, 1995 and 1997 and tested for exposure to 5 fatal canine diseases. The observed population decline was not associated with changes in seroprevalence over the period of decline. Foxes tested negative for canine distemper and 2 strains of leptospirosis and 1 fox tested positive for parvovirus in 1994. Annual seroprevalence to canine adenovirus ranged from 89-100%, similar to previous serologic studies. Canine adenovirus may be resident in the San Miguel Island fox population, as in other island fox populations, but its role in the observed fox decline is unknown.

Changes in population parameters suggested that the fate of females in the population influenced population dynamics. Overall sex ratio favored males, though annual sex ratios did not differ from parity. Recruitment into the population was correlated with pup production from the previous year. Pup production was correlated with the number of adult females, and with the number of lactating females. Female pup survival was correlated with female pup weights from the previous year. Factors affecting pup weights were not determined. Pup weights were not correlated with adult female weights or with measures of environmental variability, although a single measure of pup weight may reflect developmental constraints more than environmental influences. We observed limited evidence of negative density-dependent effects in this study. Decrease in density did not result in increases in reproductive effort or success, except that the proportion of females that lactated increased following a decline in density. Litter size did not increase following decline. Fox populations may be slow to recover following a catastrophic decline.

EXECUTIVE SUMMARY

Data from the Park's monitoring program indicates that the island fox population on San Miguel Island declined substantially in 1995 and 1996, from a high of around 450 adult fox to less than 100 (Fig. 1). The decline was first observed in 1995 on the west end of the island and then in 1996 on the east end. Though other island fox populations have shown natural fluctuations over time, the range of fluctuation on San Miguel is greater than recorded ranges from other island populations (Roemer et al. 1994). There is no apparent cause for the observed decline, but possible causes include 1) the effects of weather on food availability; 2) disease, and 3) predation.

It is possible that the observed declines are part of natural variation in fox populations, due to weather-caused changes in food availability. Island foxes are primarily insectivorous on Santa Cruz Island, and their body weights fluctuate with seasonal changes in insect availability (G. Roemer, unpubl. data). However, it is unknown how important seasonal or annual changes in insect, deer mouse (*Peromyscus maniculatis*) or vegetation abundance are in determining fox population dynamics on San Miguel Island. Deer mice, sea-fig (*Carpobrotus chilensis*), and insects are the 3 most important food items in the annual diet of foxes on San Miguel Island (Collins and Laughrin 1979). Deer mouse densities on San Miguel Island did not change over the study period. Relative cover of sea-fig, an important item in San Miguel Island fox diet, generally increased from 1984 to 1996, but did not change during the study period. We did not monitor changes in insect abundance, and it is possible that annual variation in insects may have influenced fox populations.
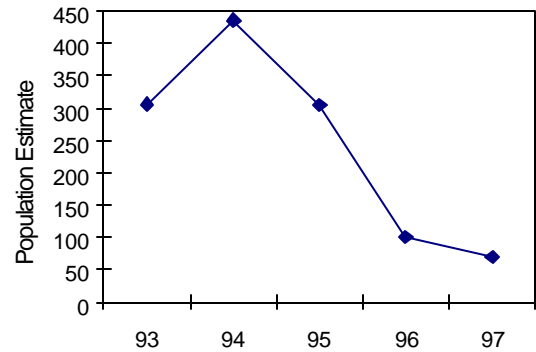

Figure 1. Annual islandwide population estimate for island fox, San Miguel Island, Channel Islands National Park (based on annual average densities from 3 grids).

Weather did not appear to affect island fox populations. Neither island fox density or survival rates were correlated with winter precipitation. Despite interannual variation in precipitation and the periodic effects of El Niño and drought, the climate of San Miguel is relatively stable compared to the other islands, and to the mainland. The persistent marine layer and associated fog reduce variability in temperature, and fog drip may be an important source of water augmenting annual rainfall. As a result, deer mouse populations are consistently higher and more stable than on other islands.

The decline in the San Miguel fox population may be due to a disease agent. The pattern of population decline (from west to east) could be explained by a disease spreading within the fox population in that same direction. Foxes on San Miguel were previously tested for exposure to canine diseases, and were shown to have antibodies for canine parvovirus and canine adenovirus (Garcelon et al. 1992). Although National Park Service regulations do not allow

domestic dogs on the island, boaters have been observed bringing dogs ashore on San Miguel Island (I. Williams, pers. comm.) and on nearby Santa Cruz Island (G. Roemer, pers. comm.). These periodic visits by domestic dogs could expose island foxes to various diseases. However, serologic surveys conducted during this study do not suggest that canine disease was a factor in the observed decline. Fox blood samples were collected in 1994, 1995 and 1997 and tested for exposure to 5 fatal canine diseases. The observed population decline was not associated with changes in seroprevalence over the period of decline. Foxes tested negative for canine distemper and 2 strains of leptospirosis. One fox tested positive for parvovirus in 1994. Annual seroprevalence (percent of blood samples testing positive) to canine adenovirus on San Miguel ranged from 89-100%, similar to previous serologic studies. Canine adenovirus can cause infectious canine hepatitis and may be resident in the San Miguel Island fox population, as in other island fox populations. Its role in the observed fox decline is unknown, particularly without clinical evidence of disease and documented mortality.

It is possible that San Miguel's large pinniped breeding colonies and haul-out sites may be a source of disease for island foxes. Little is known about the effects of such diseases on island foxes, but, generally, canine diseases are more likely to cause fox mortality than are diseases present in pinniped colonies.

Predation by golden eagles (*Aquila chrysaetos*) has been identified as contributing to a decline in island fox on a portion of Santa Cruz Island (G. Roemer, unpubl. data). The effect of predation on San Miguel foxes is currently unknown. Two golden eagles sightings were reported from San Miguel Island during the study period. One fox carcass found in 1997 was determined to be killed by golden eagles (Gary Roemer, pers. comm.).

Population characteristics observed during the decline suggest that the fate of females in the population ultimately determines island fox population dynamics on San Miguel Island. Recruitment into the population was correlated with pup production from the previous year. Pup production, in turn, was correlated with the number of adult females, and with the number of lactating females. Moreover, female pup survival, which ultimately affects recruitment and the number of adult females, was correlated with female pup weights from the previous year. Factors affecting pup weights were not determined. Pup weights were not correlated with adult female weights, nor with measures of environmental variability.

Evidence of lactation provided data on age-specific reproductive effort in females. Although relatively few (16%) Age Class 1 (yearling) fox females reproduced, about 60% of Age Class 2 and 3 females showed signs of lactation. Females appear to reproduce well into maturity, with 7 of 9 Age Class 4 females showing signs of reproduction. Thus, the apparent loss of older foxes over the study period has consequences for future recruitment into the population.

Recapture of foxes originally caught during the design phase of the vertebrate monitoring program (1985-1989) (Fellers et al. 1988) allowed us to estimate maximum age for certain island foxes. Previously, longevity of island foxes in the wild was thought to be 4-6 years. We estimated age of several individuals in this study to be 7-10 years.

Are fox populations self-regulating? That is, do they decrease reproductive effort and success at high densities, and increase effort and success at low densities? We found limited evidence of such negative density-dependent effects in this study. Decrease in density did not result in increases in reproductive effort or

success, except that the proportion of females that bred successfully (as evident by signs of lactation) increased following a decrease in density. Litter size did not increase, nor did the number of pups or yearlings produced. Fox populations may thus be slow to recover following a catastrophic decline.

We recommend that the Park support additional research to determine the factors driving island fox population dynamics on San Miguel Island, particularly those factors affecting pup survival, and the effect of predation in general.

The current terrestrial monitoring program was sufficient to detect a population decline, but could not determine the cause of the decline. The resolution of the program could be increased by establishing insect monitoring, and by periodic survey for disease.

CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

Channel Islands National Park is one of several National Park Service units serving as prototype parks for the NPS inventory and monitoring program. Accordingly, the Park has developed a comprehensive long-term ecological monitoring program for both marine and terrestrial ecosystems (Davis et al. 1994). The purpose of the monitoring program is to 1) determine present and future health of ecosystems, 2) establish empirical limits of variation in resources, 3) diagnose abnormal conditions to identify issues in time to develop effective mitigation, and 4) identify potential agents of change. The Park's monitoring program is based on population monitoring of selected taxa, such as the island fox (*Urocyon littoralis littoralis*), because populations are basic units of ecosystems which are readily measured, interpreted and managed (Davis and Halvorson 1988). Expressions of population health, such as abundance and vital rates, integrate the effects of all environmental factors, including weather, food availability, competition, predation, disease, and human disturbance.

Development of the terrestrial vertebrate protocol, including island fox, began in 1985, and the final protocol was published as a handbook in 1988 (Fellers et al. 1988, as modified by Schwemm 1995) and has been implemented annually since 1993. The island fox was a logical choice for monitoring. A diminutive relative of the mainland gray fox (*Urocyon cineroargenteus*), the island fox is found on the 6 largest of California's 8 Channel Islands. Though individuals weigh less than 2.5 kg, the fox is the largest native mammal on the islands. Due to its small population size on several islands, the fox has been listed as threatened by the state of California (California Department of Fish and Game 1987). The island fox was chosen as a key species to monitor at the Park because of its state-listed status, its apparently low population size, the general lack of

demographic information about this species, and because of the relatively high amount of public interest in this unique canid. On San Miguel Island, island fox are annually monitored on 3 grids, using standard mark-recapture techniques.

All Park monitoring protocols direct Park staff to annually collect data and present the results of the current year's monitoring in an annual report. Trend analysis and integration of data from different monitoring protocols are done periodically. Annual results of island fox monitoring have been reported (Schwemm 1995, Schwemm 1996, Austin 1996) but trend analysis of island fox monitoring data has not been accomplished to date. Thus, the purpose of this report is to analyze 5 years of island fox monitoring data for trends in population parameters, to quantify differences among years and sites, and to investigate relationships between population parameters and other ecological factors, such as food availability and weather. We are undertaking this investigation because the island fox dataset is the most complete of the terrestrial monitoring datasets and is thus most amenable to analysis, and the data thus far have suggested that the island fox population on San Miguel Island has declined precipitously during the study period.

This report quantifies temporal and spatial variation in density, pup production, recruitment, weight, survival, and sex ratio in island fox populations on San Miguel Island. We tested the following hypotheses: 1) island fox population density declined over time on the three grids; 2) changes in density were correlated with changes in food availability, weather; and exposure to lethal canine diseases; 3) pup weight was correlated with female weight; 4) pup weight influenced survival of pups to yearling stage; and, 5) negative density-dependent effects would be observed, such as increased reproductive effort and success following a decline in population density.
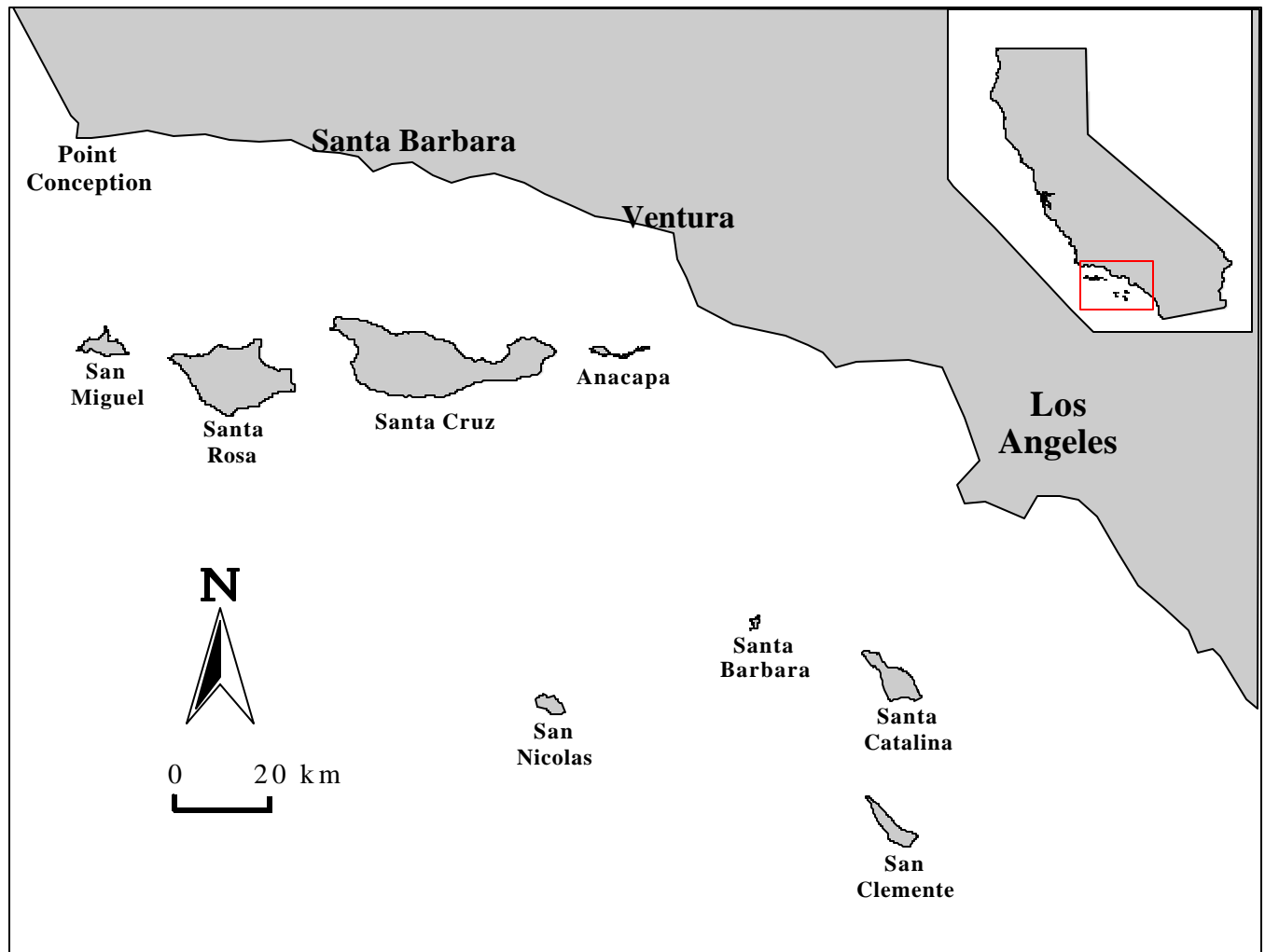
Figure 2. Channel Islands National Park, California. The Park comprises San Miguel, Santa Rosa, Santa Cruz, Anacapa and Santa Barbara Islands.

MATERIALS AND METHODS

Study Area

The California Channel Islands comprise 8 islands located at various distances from the mainland in the Southern California Bight (Fig. 2); the northern 5 islands are included in Channel Islands National Park. The islands range in size from less than 300 ha (Anacapa and Santa Barbara) to over 25,000 ha (Santa Cruz). Of the Park islands, Anacapa is closest to the mainland, being 22 km from the coast, whereas Santa Barbara lies 73 km away. The larger islands are topographically diverse, and support a variety of habitat types, ranging from annual grasslands to coastal scrub communities and oak and conifer woodlands (Halvorson et al. 1988). Island foxes occur on the 6 largest of the Channel Islands; they do not occur on Anacapa or Santa Barbara Islands.

The National Park Service monitors island fox populations on San Miguel Island, the westernmost island of the northern Channel

Islands. At 3,865 ha, San Miguel is the smallest of the islands on which island foxes occur. The island is a gently sloping plateau with long sandy beaches along the coastline. The island is fully exposed to the prevailing northwesterly wind, and is recovering from a period of severe overgrazing and erosion due to historic sheep grazing (Hochberg et al. 1979).

San Miguel's vegetation (Fig. 3) is currently dominated by grassland, which covers most of the deeper, stabilized soils on the island terrace (Hochberg et al. 1979). Introduced annuals (*Avena* spp. and *Bromus* spp.) dominate the grasslands. Native bunchgrasses such as *Nasella pulchra* occur more toward the eastern end of the island, but not in large stands. There is evidence that shrub species, particularly coyote brush (*Baccharis pilularis*), are invading some grassland areas. The second most abundant vegetation type is *Isocoma* scrub, characterized by coast

goldenbush (*Isocoma menziesii*), San Miguel Island locowed (*Astragulus miguelensis*), California saltbush (*Atriplex californica*), and coyote brush. Coastal dune scrub vegetation occurs on the coast and extends well inland in some areas. Some inland sand dune areas are dominated by dense stands of silver lupine (*Lupinus albifrons*). Large bare areas on the island can be characterized as either unstabilized dunes ("sand stripes"), which are generally being colonized by coastal dune scrub species, or as erosion pavement where the soil cover has been removed, leaving a hardpan layer. Sea cliffs are dominated by coastal bluff scrub, including, in some areas, giant coreopsis (*Coreopsis gigantea*) and in others, introduced iceplant (*Mesembryanthemum crystallinum* and *M. nodiflorum*).
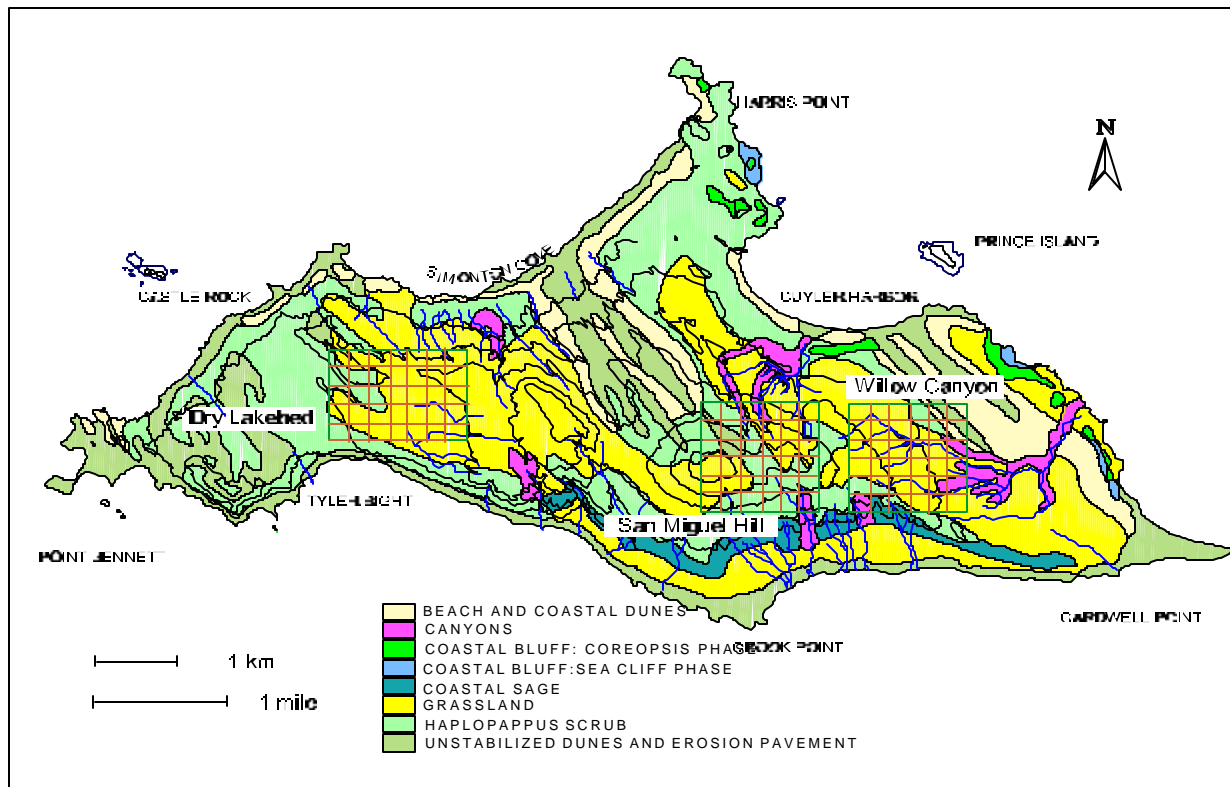
Figure 3. Vegetation communities and island fox monitoring grids on San Miguel Island.

The Dry Lakebed grid (Fig. 3) comprises primarily grassland cut by gentle ravines on the west end of the island. The western end of the Dry Lakebed grid extends onto a low area which is inundated in years of moderately high precipitation. The east end of the grid extends up the west flanks of Green Mountain.

The San Miguel Hill grid extends eastward from San Miguel Hill and is the most varied of the 3 grids, both in topography and vegetation. More than a third of the grid is grassland, a third *Isocoma* scrub, and the remainder is canyon or unstabilized dune.

The Willow Canyon grid comprises primarily grassland which is being invaded by *Baccharis*, although portions of the grid cover *Isocoma* scrub, canyon, coastal bluff scrub and unstabilized dune.

Island Fox Monitoring Methods

On San Miguel, island foxes are annually monitored on three grids. Island foxes are also monitored on one island (San Clemente) outside the Park and on another (Santa Cruz) within Park boundaries. Results from these other monitoring programs are comparable to San Miguel, since all monitoring programs employ a standardized capture-recapture protocol (Roemer et al. 1994).

Trapping

Field work was conducted in mid to late summer (July-August) from 1993 to 1997. Three island fox trapping grids (Fig. 3) have been established on San Miguel Island (Schwemm 1995). The island fox monitoring protocol originally developed for the Park (Fellers et al. 1988) established 5 trapping grids of 25 traps each (5 x 5), with trap spacing of 322 m. Upon implementation of the island fox monitoring program in 1993, the grid design was changed to

3 grids of 49 or 48 traps, and decreased spacing between traps (250 m). These changes were necessary to increase capture probabilities for foxes. The Willow Canyon and San Miguel Hill grids each have 49 traps arrayed in a 7 x 7 grid (Figure 3). The Dry Lakebed grid has 48 traps arrayed in a 6 x 8 grid. In 1993, trapping on the Willow Canyon grid was conducted with 42 traps in a 6 x 7 array.

Live traps (23 x 23 x 66 cm, Tomahawk Live Trap Co., Tomahawk, WI) were baited with dry cat food and a fruit scent (Knob Mountain Raw Fur Co., Berwick, PA). Traps were covered with burlap and placed to provide protection from sun, wind and precipitation. A "chew tube" made of refrigerator (polyethylene) tubing was wired to the inside of each trap to provide captured foxes with a soft surface to chew upon. Each grid was trapped annually for six days, except for the Dry Lakebed grid, which was not trapped in 1993. During trapping, traps were checked once during every 24-hr period.

Marking and handling

Upon first capture, foxes were weighed (± 25 g), and sex, age, reproductive condition, presence of ectoparasites, and injuries were recorded. Foxes were aged according to tooth eruption and wear patterns on the first upper molar (Wood 1958) and were assigned to discrete age classes (G. Roemer, pers. comm.). Foxes were classified as pups (Age Class 0), young adults (Age Class 1: ca. 7 months to 2 years), adults (Age Class 2: ca. 2 to 3 years), mature adults (Age Class 3: ca. 3-4 years old) and old adults (Age Class 4: >4 years old).

Foxes were marked with colored ear tags (Nasco-West, Modesto, CA) inserted in the pinna and/or passive integrated transponder (PIT) tags (Biosonics, Seattle, WA) inserted subcutaneously between and just anterior to the scapulae. During the course of the study we shifted from use of ear

tags to use of PIT tags because the latter have a lower loss rate (Schwemm 1996), result in fewer injuries to foxes, and are inconspicuous.

During the study we caught foxes which had been marked during the design phase of the monitoring program (Fellers et al. 1988). These foxes were originally caught from 1985 to 1989 and were marked with collars made from 12 mm wide plastic cable ties. Collars were securely attached around the neck, and an identification number was permanently etched on the collar.

Estimation of Density and other Population Parameters

Island fox population sizes were estimated annually for each grid using closed population models from the program CAPTURE (version 2, White et al. 1982) as described by Roemer et al. (1994). Because CAPTURE's models for population size do not work well with very small population sizes, Chapman's modification of the Lincoln-Peterson (LP) estimator was used to calculate population size for the Dry Lakebed grid in 1996.

Island fox density was estimated using the mean maximum distance moved (MMDM) method (Wilson and Anderson 1985). Naïve (or crude) density is calculated according to $D = N/A$, where N is the estimate of population size and A is the area of the trapping grid. Although closed population models assume that populations are closed both demographically and geographically, the naïve density estimator does not account for "edge effect" resulting from incomplete geographic closure. The size of the area trapped is actually larger than the size of the grid, due to the movements of animals residing on or just outside the grid. To account for this, the effective trap area A(W), where W is the boundary strip around the grid, was determined using estimates of MMDM provided by CAPTURE. MMDM is a measure of the maximum distance an animal

moves between successive captures. A(W) was estimated by adding ½MMDM to all sides of a grid. Density was estimated for each grid by dividing N by A(W). Standard errors of density estimates and 95% confidence intervals were estimated using the methods of Wilson and Anderson (1985). To estimate annual islandwide population of adult foxes, average annual density from the 3 grids was multiplied by the island area (38.7 km^2).

Density of adult foxes (classes 2, 3 and 4) was estimated for all grids and years, because adult density is a more conservative indicator of population change than total density. Pups were thus excluded from density estimates to reduce the variability introduced by interannual variation in pup survival.

Pup productivity was calculated as the number of pups recorded annually on each grid. Recruitment was estimated as the number of young adults, or Age Class 1 individuals. Sex ratios were calculated for pups and adults.

Adult and pup survival rates were estimated with program MARK (White and Burnham 1997), which uses individual encounter histories to provide estimates of apparent survival for populations of marked animals. Apparent survival is the probability of recapturing an animal between encounter sessions. Apparent survival does not account for emigration, and thus may underestimate true survival, which is the probability of surviving between encounter sessions.

We investigated differences in apparent survival between sexes, between adults and pups, and between areas. For survival analysis, we pooled data for the Willow Canyon and San Miguel Hill grids, since there was considerable movement of individual foxes between those grids. During the study period, 23 foxes moved between the San Miguel Hill and Willow Canyon grids, as indicated

by recaptures. In contrast, only 1 fox moved between the Dry Lakebed grid and any other grid during the study period.

Food Availability

Data from the Park's long-term ecological monitoring program (Schwemm 1995, 1996; Austin 1996) were used as indices of population trend for vertebrate prey and vegetation food items. Collins and Laughrin (1979) report that island foxes on San Miguel Island are opportunistic omnivores, consuming a wide variety of plants and animals. Summer and fall diets comprised insects and the fruits and leaves of sea-fig, or iceplant (*Carpobrotus chilensis*), whereas winter diets were characterized by deer mice (*Peromyscus maniculatus*), birds, insects and iceplant.

Spring and fall densities of deer mice were estimated with capture-recapture data from permanent grids (Fig. 4). Each grid comprises 100 Sherman traps in a 10 x 10 configuration, with 7 m spacing between traps.

Herpetofauna were sampled several times annually on permanent cover board transects (Fig. 4). Each transect comprises two lines of 30, 1 ft^2 boards, spaced 5 m apart. An index of seasonal abundance was calculated for alligator lizards *(Elgaria multicarinata multicarinata)* as number of individuals per 30 boards. The cover board method does not capture sufficient numbers of western fence lizards (*Sceloporus occidentalis becki*) to use as a population index (Fellers et al. 1988).

Data on relative abundance of ground-nesting birds is available from the Park's landbird monitoring program (Coonan 1995, 1996). Birds were monitored in spring and fall along permanent line transects that utilize the island's trail system (van Riper et al.1988). All birds within 100 m of the transect midline were recorded.

Relative cover of sea-fig was used as an index of availability for sea-fig fruits and leaves, though we do not know if sea-fig fruit and leaf availability is correlated with sea-fig relative cover. Data from the Park's vegetation monitoring program (Halvorson et al. 1988) were used to calculate relative cover of sea-fig. Vegetation was monitored annually on 16 permanent transects on San Miguel Island. Each 30 m transect comprises 100 points at which vegetation cover of all species is recorded. Relative cover of sea-fig was calculated as the number of sea-fig hits on each transect. Relative cover was averaged for habitat types with multiple transects. Data on abundance of insects and other arthropods is not available.

Weather

Daily precipitation, daily maximum temperature, and daily minimum temperature were obtained from the daily weather log maintained at the Nidever Canyon Ranger Station, San Miguel Island. From these data, monthly precipitation, monthly mean maximum temperature, and monthly mean minimum temperature were calculated.

Although our precipitation data for San Miguel Island were insufficient to evaluate interannual trends, the precipitation record from neighboring Santa Rosa Island dates from the 1940's. Annual precipitation was San Miguel Island was correlated with annual precipitation from Santa Rosa Island ($r^2 = 0.793$, F = 11.505, p = 0.043), and so we used the latter to evaluate interannual variation in precipitation.

Exposure to Canine Diseases

Fox blood samples were collected and tested for presence of antibodies to 5 lethal canine diseases. Three to 10 ml of blood were drawn from the femoral vein of unanesthetized captured foxes. Sera was obtained from 22 foxes in 1994,

15 foxes in 1995, and 18 foxes in 1997. Serum was separated from the cellular fraction by centrifugation, removed, and then frozen. Sera were tested for antibodies against canine adenovirus, canine distemper, canine parvovirus, *Leptospira canicola*, and *Leptospira ictero*. Serologic tests were conducted at the Washington Animal Disease Diagnostic Laboratory Washington State University, Pullman, Washington 99164. Antibody titers of ≥ 1:5 were considered evidence of previous exposure to canine adenovirus and canine distemper virus. Antibody titers of ≥ 1:25 were considered evidence of previous exposure to canine parvovirus. Antibody titers of ≥ 1:100 were considered evidence of previous exposure to *Leptospira canicola* and *Leptospira ictero*. Seroprevalence for each disease was calculated as the percentage of the total number of samples which tested positive.

Statistical Analysis

Differences among years and sites were evaluated with analysis of variance (ANOVA) and with chi-square tests (SYSTAT 7.0, SPSS Inc.,

1997). Because island fox density estimates for each grid and year were not replicated, analysis of variance could not be conducted to test for differences among years and grids. Instead, contrasts (Steel et al. 1997) were used to test for differences in fox densities among years. Contrasts were also used to compare deer mouse density estimates among years.

Simple linear regression was used to test relationships between variables. Because pups gain weight over the sampling season, analysis of covariance (Neter et al. 1996) was used to estimate differences among years and between sexes for pup weights, with Julian date as the covariate. Repeated measures analysis of variance (rmANOVA, SYSTAT 7.0) was used to evaluate differences in relative cover of sea-fig and landbirds over time.

Percent or proportion data were transformed with the arcsine function prior to analysis. Significance levels were set at 0.05 for all tests except contrasts for comparison of density estimates, for which significance levels were set at 0.10, in order to minimize the chance of a type 2
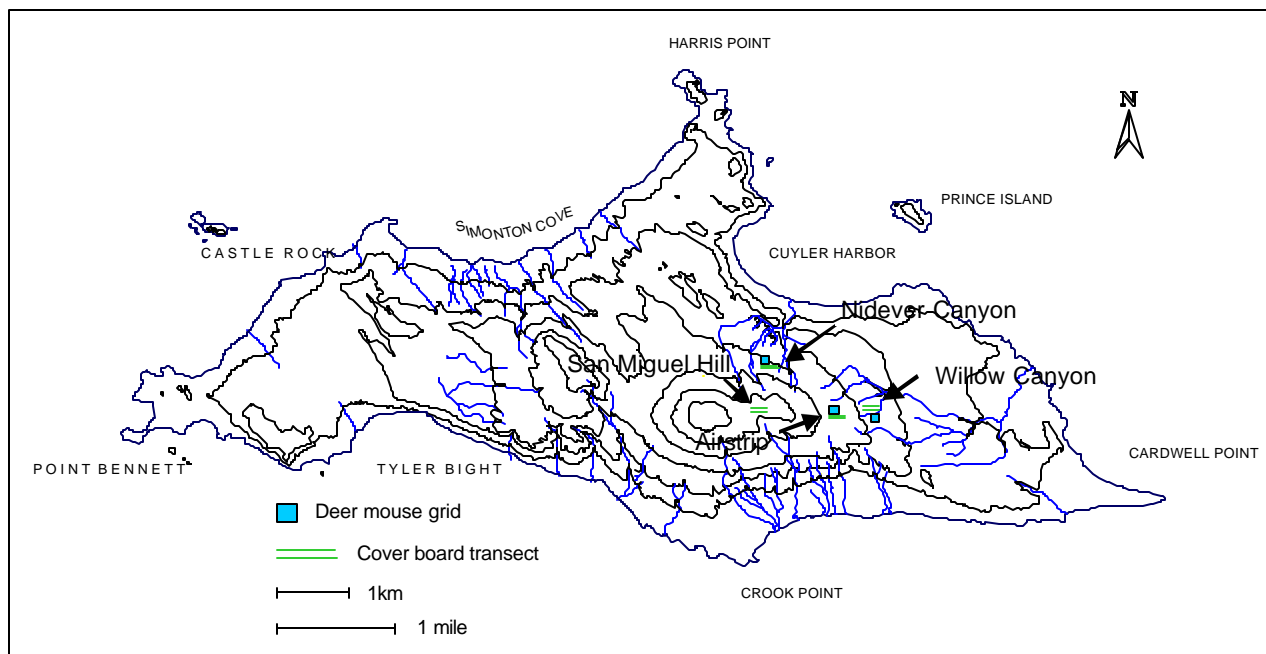
Figure 4. Locations of deer mouse grids and lizard cover board transects, San Miguel Island.

error (failing to detect a decrease in density). In a long-term ecological monitoring program, failing to detect a problem (type 2 error) is at least as serious as a false report (type 1 error) (P. Geissler, USGS-BRD, pers. comm., Steidle et al. 1997).
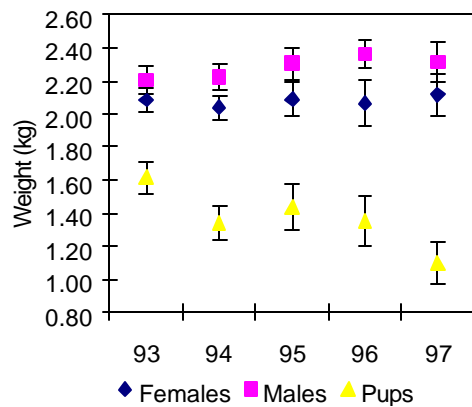
Figure 5. Annual average weights of island foxes, San Miguel Island.

RESULTS

Weights

Average weights for adult (Age Classes 2, 3 and 4) males, adult females, and pups are shown in Fig. 5. Average adult male weight over the 5 year period was 2.25 kg (n = 142, SE = 0.023). Average female adult weight was 2.06 kg (n = 118, SE = 0.024). Adult male weights did not differ among sites (F = 0.002, p = 0.998) or years (F = 0.913, p = 0.341), nor did adult female weights differ by site (F = 0.353, p = 0.703) or
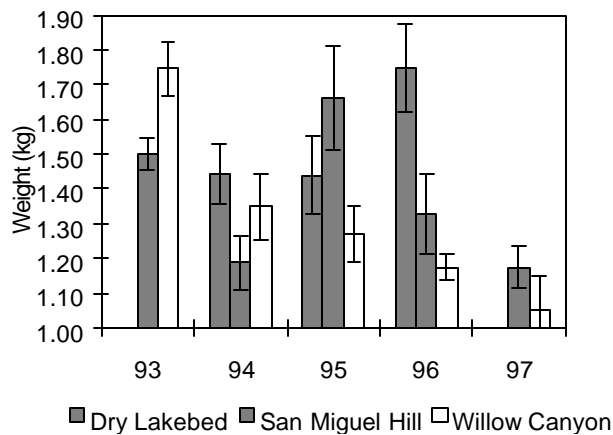
Figure 6. Average weights of island fox pups, San Miguel Island.

year (F = 0.639, p = 0.426).

Average pup weight was 1.43 kg (n = 97, SE = 0.033). Pup weights differed by year (F = 2.675, p = 0.036) but not by sex (F = 0.748, p = 0.389) when ANOVA was run with Julian date as a covariate. The interaction between year and Julian date was also significant (F = 2.488, p = 0.048), suggesting that pups gained weight at different rates in different years. Pup weights were not correlated with adult female weight (F = 1.152, p = 0.306), or with annual precipitation (F = 0.011, p = 0.924).
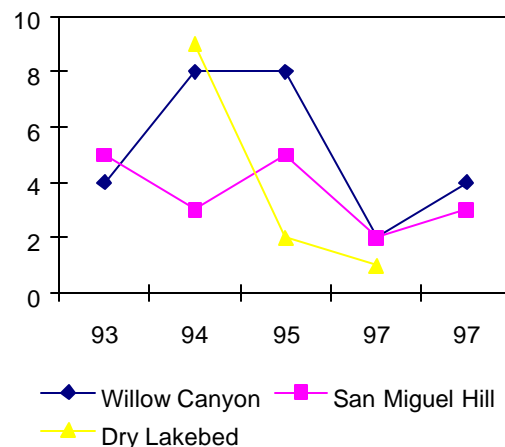
Figure 7. Number of lactating females on each grid, San Miguel Island.

Reproduction and Recruitment

Measures of reproductive effort include number of lactating females, proportion of females that lactated, and litter size. The number of lactating females on each grid (Fig. 7) was highly correlated with density ($r^2 = 0.710$, F = 30.324, p < 0.001) and with number of adult females ($r^2 = 0.759$, F = 38.714, p < 0.001), and decreased as density decreased.

Table 1. Proportion of females that lactated, by age class.

Age Class	1993	1994	1995	1996	1997	Total
1	0.00 (0/7)	0.16 (4/25)	0.25 (4/16)	0.00 (0/2)		0.16 (8/50)
2	0.75 (3/4)	0.53 (9/17)	0.64 (7/11)	0.75 (3/4)	0.67 (2/3)	0.62 (24/39)
3	0.75 (3/4)	0.20 (1/5)	0.60 (3/5)	0.00 (0/2)	1.00 (5/5)	0.57 (12/21)
4	0.50 (1/2)	0.83 (5/6)	1.00 (1/1)			0.78 (7/9)
Total	0.44 (7/16)	0.36 (19/53)	0.45 (15/33)	0.38 (3/8)	0.88 (7/8)	0.43 (51/119)

We expected reproductive effort to increase following low densities, but such negative density-dependent effects were not evident in regressions of reproductive effort (proportion of females that lactated and litter size) with current density measures. Although 7 of 8 adult females lactated in 1997, when densities were lowest, the proportion of adult females that lactated on each grid was not correlated with grid density (F = 2.727, p = 0.127), or with numbers of adults, (F = 2.279, p = 0.130), nor with number of adult females (F = 3.610, p = 0.084). However, the proportion of females that lactated was negatively correlated with density from the previous year(r^2 = 0.378, F = 6.475, p = 0.034), suggesting that there may be a lag time before negative density-dependent effects are observed.

When data from all grids were pooled, the proportion of females that lactated (Table 1) differed by age class (c^2 = 26.516, df = 3, p < 0.0001) but not by year (c^2 = 7.778, df = 4, p = 0.10). Only 16% of Age Class 1 females lactated, whereas 62% of Age Class 2 females lactated, and 57% of Age Class 3 females lactated. Seven of 9 Age Class 4 females lactated.

Litter size on each grid (Table 2) was not correlated with density (F = 2.608, p = 0.135) or with number of adult females (F = 2.802, p = 0.122), or with previous year's density (F = 0.899, p = 0.371).

Table 2. Litter size (number of pups/number of lactating females), San Miguel Island.

	Willow Canyon	San Miguel Hill	Dry Lakebed
1993	2.75	2.40	--
1994	2.00	3.00	1.22
1995	1.38	1.60	2.50
1996	3.00	2.50	3.00
1997	2.00	1.33	
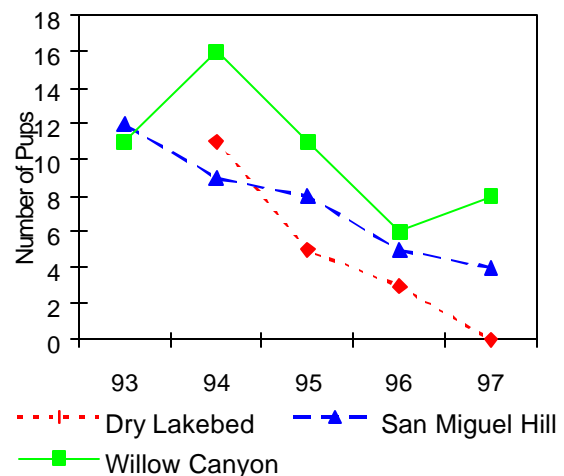
Figure 8. Total numbers of island fox pups captured on each of 3 trapping grids, San Miguel Island.

Measures of reproductive success include number of pups and recruitment, or the number of pups that survive to yearling, or young adult, stage. The number of pups captured on each grid generally declined from 1993 to 1997 (Fig. 8). The number of pups on each grid was positively correlated with adult density (r^2 = 0.516, F =

13.795, p = 0.003), with number of adult females ($r^2 = 0.567$, F = 16.697, p = 0.002), and with number of lactating females ($r^2 = 0.637$, F = 22.064, p = 0.001).
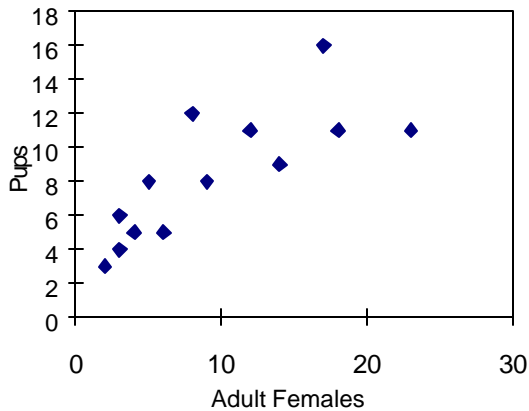
Figure 9. Island fox pups versus adult females, San Miguel Island.

Although the number of pups increased with increasing numbers of adults, adult females, and with increasing density, the number of pups appeared to level off at high density levels (Fig. 9).

The number of young adults, or pups that have survived to Age Class 1 (Fig. 10), is a better indicator of recruitment than number of pups, since the latter does not account for variable pup survival. Number of young adults increased on the Willow Canyon grid from 1993 to 1995 but declined in 1996 and 1997. On the San Miguel Hill grid, number of young adults increased in 1994 but declined thereafter. Number of young adults declined on the Dry Lakebed grid from 1994 to 1997. The number of young adults on each grid was strongly correlated with the number of pups from the previous year ($r^2 = 0.751$, F = 31.108, p < 0.001).

Survival and Age Distribution

The age distribution of island fox changed over the study period on all grids (Fig. 11). During that period, mature foxes (Age Class 3) and older foxes (Age Class 4) virtually disappeared from all grids. However, 2 Age Class 3 individuals and 2 Age Class 4 individuals were recaptured in 1997 after being apparently absent from the grids for 2-4 trapping seasons.

The survival of several cohorts of pups can be tracked on the Willow Canyon and San Miguel Hill grids. Pups dominated the 1993 distribution for San Miguel Hill, and that cohort dominated the 1994 age distribution as members of Age Class 1. However, that cohort did not survive well into the following year. Both Age Class 1 and Age Class 2 individuals decreased on San Miguel Hill from 1994 to 1995. Likewise, a large cohort of pups on the Willow Canyon grid in 1994 is reflected in the Age Class 1 distribution for 1995, but not in Age Classes 1 or 2 in 1996. Low numbers of young adults, or Age Class 1 individuals, were recorded in 1997, reflecting poor pup survival from 1996 to 1997.
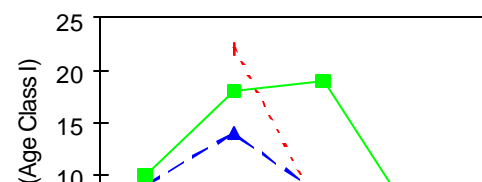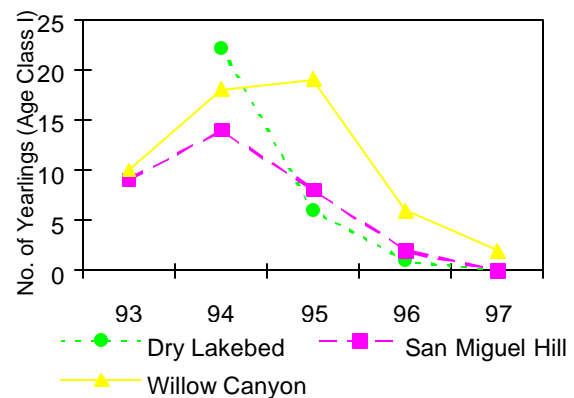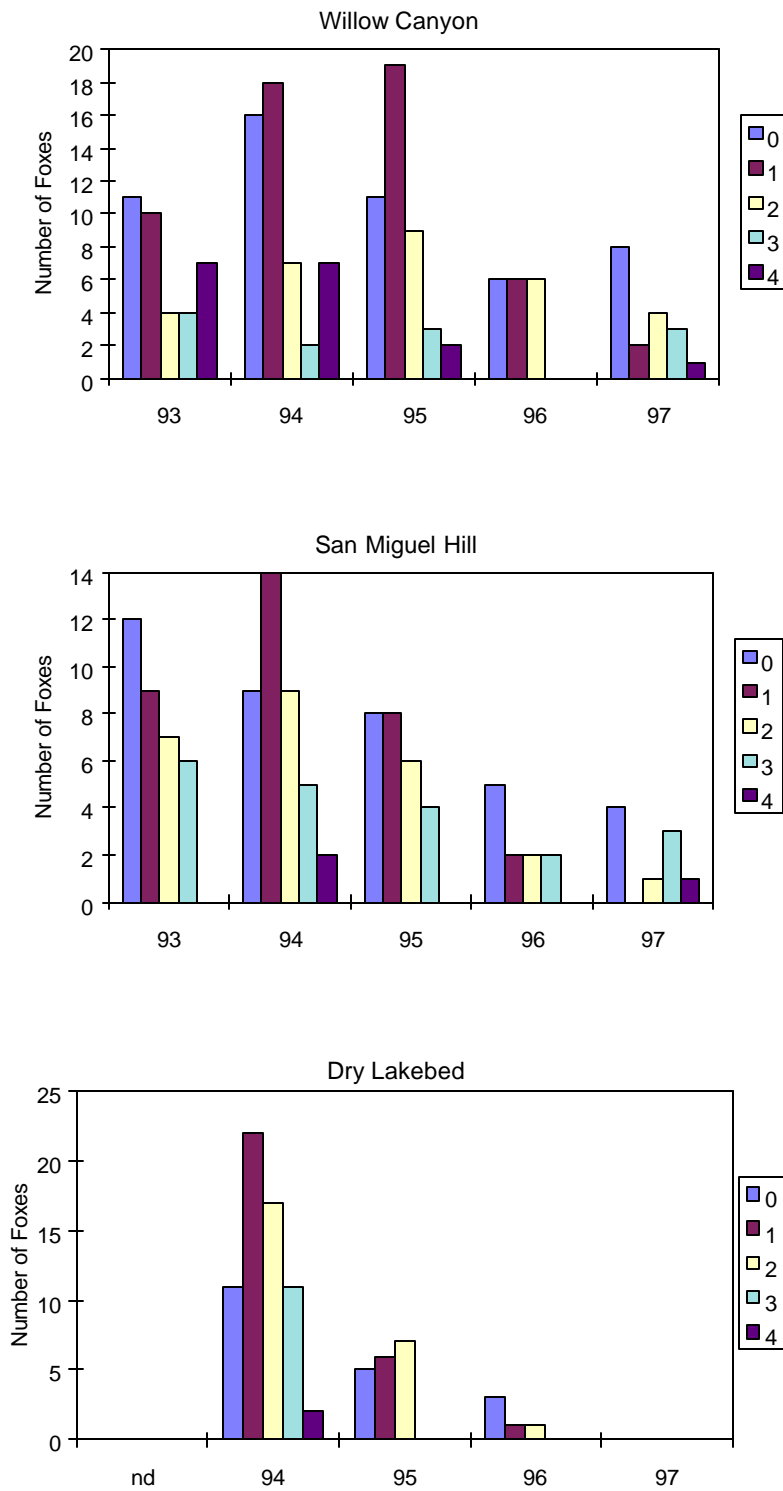
Figure 11. Distribution by age class of island fox, San Miguel Island (nd = no data).

Table 3. Adult fox survival estimates, San Miguel Island. Estimates are from program MARK (White and Burnham 1997).

Year	East[1]		West	
	Survival	SE	Survival	SE
1993	0.931	0.137		
1994	0.491	0.094	0.471	0.056
1995	0.501	0.173	<0.001	<0.001
1996	0.577	ne[2]	<0.001	ne

[1]East = Willow Canyon and San Miguel Hill grids; West = Dry Lakebed grid

[2]ne = not estimated; insufficient data to calculate standard error

Because adult survival did not differ by sex for either the east end (Willow Canyon and San Miguel Hill grids) or the west end (Dry Lakebed grid), both male and female capture histories were used to estimate adult survival (Table 3, Fig. 12). Adult survival on the Willow Canyon/San Miguel Hill grids was >90% from 1993 to 1994, but then declined to around 50% for the subsequent years. Chi-square analysis indicated a significant difference among years for adult survival on the Willow Canyon/ San Miguel Hill grids ($\chi^2 = 17.582$, df = 3, p = 0.001).

Adult survival on the Dry Lakebed grid was similar to the Willow Canyon/ San Miguel Hill grids for 1994-95, but then declined to < 0.001 in subsequent years. On the Dry Lakebed grid, no previously captured foxes were recaptured during monitoring in 1996 or 1997. During 1997, no foxes were captured at all on the Dry Lakebed grid.

In contrast to adult survival rates, pup survival rates differed between sexes for the Willow Canyon/ San Miguel Hill grids (Fig. 13). Female pup survival on those grids varied among years ($\chi^2 = 15.596$, df = 3, p = 0.001) and declined over the study period. Of the 5 female pups captured in 1996, none were captured in 1997. Male pup survival on those grids did not vary over time ($\chi^2 = 4.775$, df = 3, p = 0.189).
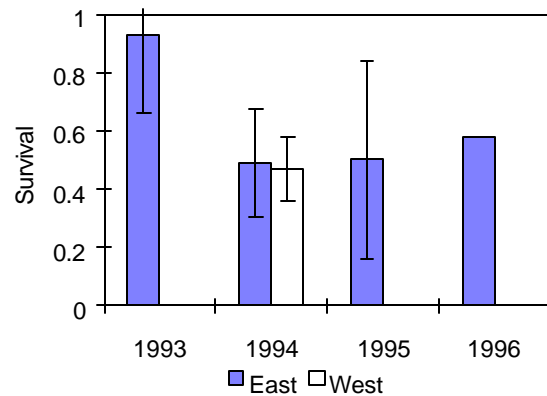
Figure 12. Adult fox survival estimates, from program MARK (White and Burnham, 1997).

Program MARK was not used to estimate survival for pups on the Dry Lakebed grid, because no pups were ever recaptured on that grid. This includes 11 pups initially captured in 1994, 5 in 1995, and 3 in 1996. Pup survival on the Dry Lakebed grid was apparently 0 for all years.

Female pup survival on the Willow Canyon and San Miguel Hill grids was strongly correlated with female pup weights from the previous year ($r^2 = 0.924$, F = 37.322, p = 0.026). That is, female pup survival declined over the study period as female pup weights declined. Male pup survival was not correlated with previous male pup weights (F = 0.214, p = 0.689).

During the study period we captured foxes which had originally been captured and marked with permanent plastic collars during the design phase of the monitoring program, from 1985 to 1989. Estimated age for these foxes, based on their estimated age at date of first capture, was 7-10 years (Table 4).

Figure 13. Pup survival rates for the east end of San Miguel Island (Willow Canyon and Dry Lakebed grids). Survival estimates are from program MARK (White and Burnham 1997).

Table 4. Estimated age (in years) of island foxes on San Miguel Island.

Collar #	Date First Caught (Estimated Age)[1]	Date Last Caught	Estimated Age
1050	10/5/85 (1)	7/21/94	10
1080	10/6/85 (1)	8/1/93	9
1110	11/6/88 (2)	8/10/94	8
1113	10/11/88 (pup)	7/21/95	7
1114	11/5/88 (2)	8/10/94	8
1116	10/9/88 (2)	7/19/94	8
1117	11/7/88 (3)	7/19/94	9
1118	1/9/89 (2-3)	7/20/95	8-9

[1] Gary Fellers, unpubl data

Sex Ratios

For both adults and pups, more males than females were recorded for all years except 1995, when more adult females than adult males were recorded (Tables 5 and 6). None of the annual sex ratios for adults or pups differed significantly from 1:1.

Overall pup sex ratio was 1.37:1, which was not significantly different from 1:1 (χ^2 = 2.651, p = 0.103). Overall adult sex ratio was 1.20:1, which was not significantly different from 1:1 ($\chi^2 = 2.042$, p = 0.103). Pup sex ratio did not differ significantly from adult sex ratio ($\chi^2 = 0.350$, p = 0.554). However, when data were pooled for all years, grids, and age classes, overall sex ratio (males:females) was 1.24:1, which differed significantly from 1:1 ($\chi^2 = 4.348$, p = 0.037), probably due to increased sample size.

Table 5. Annual sex ratios of adult and pup island fox on all grids, San Miguel Island. Sex ratio value is number of males per 1 female.

	1993	1994	1995	1996	1997	TOTAL
Adults						
Males	29	60	30	12	10	141
Females	16	53	33	8	8	118
Sex Ratio	1.81	1.13	0.91	1.5	1.25	1.20
Pups						
Males	14	22	14	8	5	63
Females	9	14	10	6	7	46
Sex Ratio	1.55	1.57	1.40	1.33	0.71	1.37

Adult sex ratio did not differ by year, grid, or age class. Pup sex ratio (Table 6) did not differ by year, but difference by grid was almost significant (χ^2 = 5.179, p = 0.075). More male than female pups were recorded on both the Willow Canyon and San Miguel Hill grids, but more females than males were recorded on the Dry Lakebed grid. When data were pooled for all years, pup sex ratio for San Miguel Hill was significantly greater than 1:1. When data from Willow Canyon and San Miguel Hill were pooled, pup sex ratio was 1.65:1, which also differed from parity (χ^2 = 5.378, p = 0.020).

Population Size and Density

Annual population size and density were estimated for each grid (Fig. 14, Table 7). To avoid counting animals twice, foxes that were captured on more than one grid in a given year were counted only on the grid where they were captured more frequently. This occurred only between the Willow Canyon and San Miguel Hill girds, which are contiguous. The number of adult foxes captured on both grids and subsequently assigned to one grid for 1993-1997 was 5, 2, 3, 4, and 1, respectively.

Overall, density generally declined over time. Density increased on the Willow Canyon grid from 1993 to 1995 but declined in 1996 and 1997. Density on the San Miguel Hill grid stayed the same from 1993 to 1994 but declined thereafter. Density on the Dry Lakebed grid declined from 1994 to 1997. The rate of decline was similar on the three grids from 1995 to 1996 (approximately 5-6 foxes/km^2).

Table 6. Sex ratios of island fox pups for each grid, pooled for 1993-97. Sex ratio value is number of males per 1 female.

	Willow Canyon	San Miguel Hill	Dry Lakebed
Male	30	26	7
Female	22	12	12
Sex Ratio	1.36	2.42*	0.58

*Ratio differs significantly from 1:1 (χ^2 = 5.158, p = 0.023)

Table 7. Total number of adults captured, population estimate (SE), model used, effective trap area [A(W)], density estimate, standard error, and 95% confidence interval for island fox trapping grids on San Miguel Island.

Grid/Year	No. of Adults	Population Estimate	Model[1]	A(W) km^2	Density foxes/km^2	SE	95% CI
Dry Lakebed							
1994	53	54 (1.6)	M(bh)	3.41	15.9	0.47	14.9-16.8
1995	14	21 (4.9)	M(h)	3.58	5.9	1.37	3.2-8.6
1996	2	2	n/a	n/a	0.9	n/a	n/a
1997	0	--					
San Miguel Hill							
1993	27	27 (0.1)	M(bh)	3.38	8.0	0.04	7.9-8.1
1994	27	27 (0.5)	M(bh)	3.34	8.1	0.15	7.8-8.4
1995	21	23 (3.2)	M(h)	3.40	6.8	0.93	4.9-8.6
1996	6	8 (1.8)	M(h)	4.67	1.7	0.39	1.0-2.5
1997	8	16(5.3)	M(h)	5.70	2.8	0.92	1.0-4.6
Willow Canyon							
1993	26	28 (2.9)	M(bh)	3.59	7.8	0.80	6.2-9.4
1994	27	34 (7.3)	M(bh)	3.45	9.9	2.10	5.7-14.0
1995	28	34 (4.2)	M(h)	3.09	11.0	1.36	8.4-13.7
1996	13	17 (3.6)	M(h)	3.26	5.2	1.12	3.0-7.4
1997	10	12 (3.2)	M(h)	4.61	2.6	0.69	1.3-3.0

[1]Refers to model used by program CAPTURE (White et al 1982) to estimate population. M(h) = heterogeneous capture probability model; M(bh) = combination of behavior model and heterogeneous capture probability model. n/a = number of captures too small to use CAPTURE; Chapman's modifier of the Lincoln-Peterson estimator (Lancia et al. 1996) used instead

Differences in density among years were tested with contrasts (Steel et al. 1997) for all three grids. The 1996 and 1997 density estimates for San Miguel Hill were significantly lower than the density estimates for 1993, 1994 and 1995 (t = 9.12, p < 0.05). Similarly, the 1996 and 1997 density estimates for Willow Canyon were significantly lower than the density estimates for 1993, 1994 and 1995 (t = 5.19, p < 0.10). The density estimate for the Dry Lakebed in 1995 was significantly lower than the density estimate for 1994 (t = 6.92, p < 0.05). The 1996 and 1997 Dry Lakebed density estimates were not used in contrasts, since associated variances could not be calculated.

Average islandwide population estimate for adults fell from near 500 in 1994 to less than 100 in 1997 (Table 8).
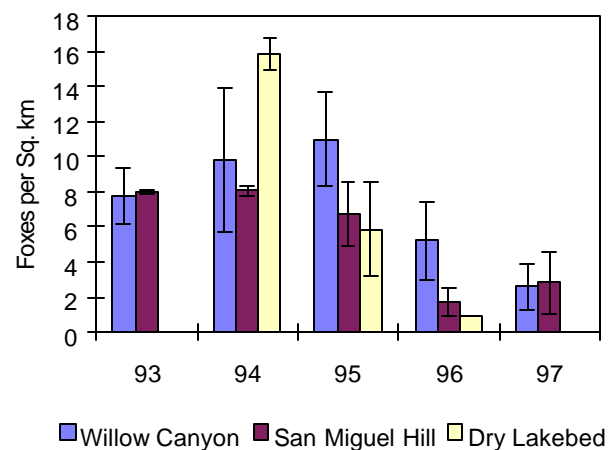
Figure 14. Estimated population density of adult island foxes, San Miguel Island.

Table 8. Annual average density and islandwide population estimates for island fox, San Miguel Island.

	Average Density	SE	Estimated Islandwide Population	95% CI
1993	7.89	0.27034	305	298-313
1994	11.26	1.16495	436	258-614
1995	7.88	0.95661	305	185-425
1996	2.61	0.87449	101	1-202
1997	1.80	0.72222	70	1-138

Table 9. Number of alligator lizards (*Elgaria multicarinata multicarinata*) caught on cover board transects, San Miguel Island, 1993-1996.

		1993		1994		1995		1996	
Site	Habitat Type	Apr	Dec	Jan	Apr	Feb	Oct	Apr	Oct
Air Strip	*Haplopappus*	0	10	16	4	15	5	1	9
Nidever Canyon	Lupine Scrub	0	ns[1]	2	1	ns	ns	0	2
Willow Canyon	Grassland	0	ns	0	0	0	0	0	1

[1]ns = not sampled

Food Availability

Number of alligator lizards captured on cover board transects was used as an indicator of lizard abundance. There was no apparent decline in the number of alligator lizards caught on cover board transects (Table 9). Differences among sites, habitats and years could not be tested without associated variances. Alligator lizard abundance appeared to differ by habitat type. Alligator lizards were almost never caught in annual grassland habitat and were rarely caught in lupine scrub habitat, but were frequently caught in *Isocoma* scrub habitat. On a seasonal basis, the number of lizards was higher in fall and winter than in spring. Annual trends are not obvious from the limited data.

Limited data on deer mouse populations (Figs. 15 and 16) indicate possible differences among grids (perhaps due to habitat differences)
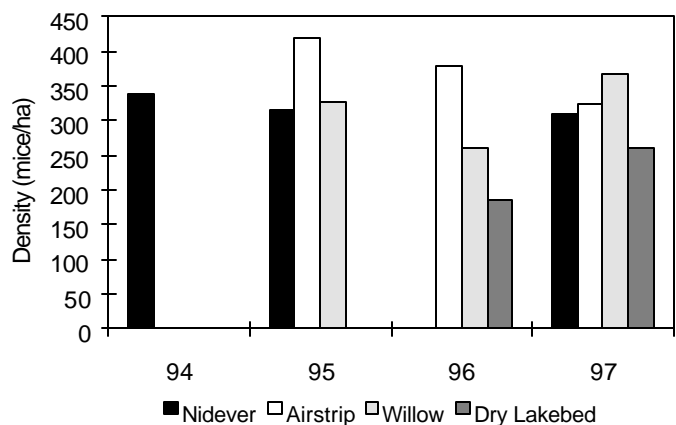
Figure 15. Fall deer mouse *(Peromyscus maniculatus)* densities, San Miguel Island, 1994 to 1996.

and seasonal differences, but do not suggest a difference in annual population trend from 1994 to 1997. Linear contrasts failed to detect changes over time for fall mouse densities or spring mouse

densities on the Nidever, Airstrip and Willow Canyon grids. During the same time period, fall deer mouse density estimates for Santa Barbara Island fluctuated between <5 and >650 mice/ha

Table 10. Relative abundance (total count) of ground nesting birds on San Miguel Island, 1993 to 1997.

Species	1993	1994	1995	1997
Horned lark (*Eremophila alpestris*)	136	95	49	27
Western meadowlark (*Sturnella neglecta*)	39	47	53	39

(Schwemm 1995, Schwemm 1996, Austin 1996).

Total numbers of ground nesting birds (Table 10) did not decline over time (rmANOVA, F = 2.140, p = 0.165). Total counts of horned larks appeared to decline steadily, but this apparent decline was not significant (rmANOVA, F = 2.434, p = 0.163).

Relative cover of sea-fig, or iceplant, generally increased on San Miguel Island between 1984 and 1996 (Fig. 17). On 6 permanent vegetation transects, sea-fig cover increased from 1984 to 1996 (rmANOVA, F = 5.572, p < 0.001). The increase after 1990 may reflect the higher precipitation during this period, in contrast to the drought years preceding this. During the study period, sea-fig cover did not change over time (rmANOVA, F = 1.187, p = 0.334). Sea-fig appeared to increase from 1993 to 1995 in all habitat types, and appeared to decline from 1995 to 1996 in island chaparral and coastal dune habitat types. It is not known whether this affected availability of sea-fig fruits and leaves as food items for island foxes. Overall, island fox densities on the three grids were not related to sea-fig cover (n = 13, F = 0.780, p = 0.394).

Weather
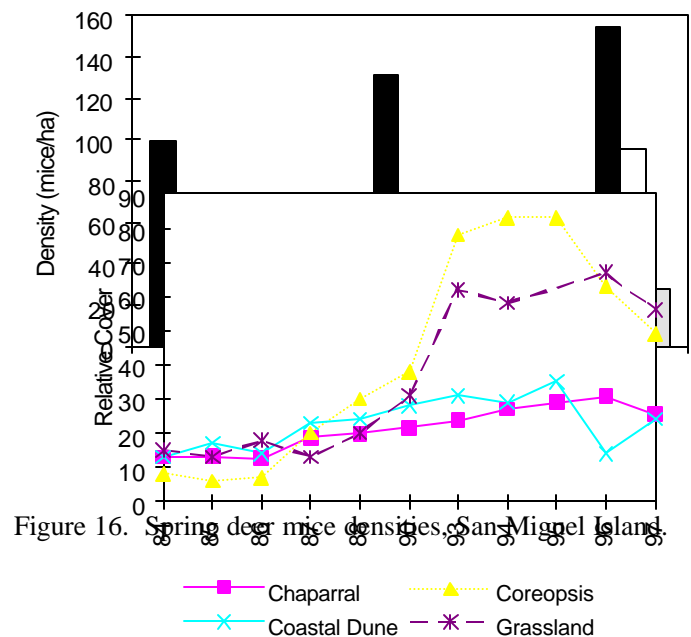
Figure 16. Spring deer mice densities, San Miguel Island.

Figure 17. Relative cover of sea-fig, or iceplant (*Carpobrotus chilensis*) in different vegetation communities, San Miguel Island, 1984 to 1996.
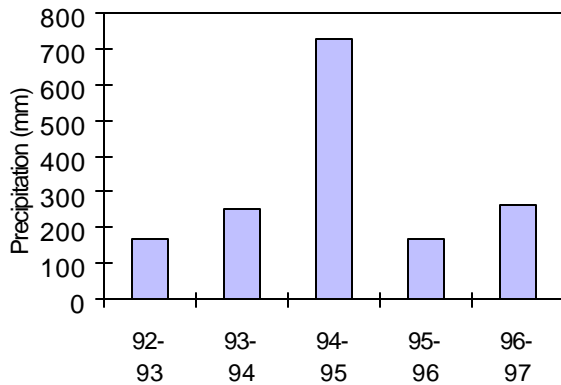
Figure 18. Winter (Oct.-Apr.) precipitation, Nidever Canyon Ranger Station, San Miguel Island.

Although winter precipitation varied from 1993 to 1997 (Fig. 18), fox densities on the Willow Canyon and San Miguel Hill grids were not correlated with previous winter precipitation

(Willow Creek: F = 1.484, p = 0.310; San Miguel Hill: F = 0.192, p = 0.691), nor were pup survival, adult male survival, or adult female survival. Annual precipitation on Santa Rosa Island from 1942 to 1996 averaged 369 mm but varied from 125 mm to 1100 mm (Fig. 19).

Exposure to Canine Diseases

Of the 5 diseases tested, antibodies were detected only for parvovirus and canine adenovirus (Table 11). Seroprevalence to canine adenovirus was high in all years tested, and was similar to seroprevalence in 1988 (Garcelon et al. 1992). Antibodies to canine parvovirus were detected in 2 of 22 samples from 1994, but not in any samples from 1995 or 1997. Seroprevalence to canine parvovirus was 30% (7/23) in 1988.

Figure 19. Annual (July 1 - June 30) precipitation, Becher's Bay, Santa Rosa Island. Data from Vail & Vickers' ranch records.

Table 11. Prevalence of serum antibodies to canine diseases in island foxes, San Miguel Island.

		1988[1]	1994	1995	1997
	n	23	22	15	18
Canine adenovirus		96[2]	95	100	89
Canine distemper		0	0	0	0
Canine parvovirus		30	9	0	0
Leptospira canicola		0	0	0	0
Leptospira ictero		0	0	0	0

[1] data from Garcelon et al. 1992

[2] Prevalence = (Number of positive samples/total number of samples tested) x 100

DISCUSSION

Island Fox Population Decline

We documented an abrupt decline in the island fox population on San Miguel Island from 1994 to 1996. Though other island fox populations have been shown to fluctuate, the range of the decline on San Miguel Island was greater than that reported for other island fox populations. Fox populations on San Clemente and Santa Catalina islands have fluctuated over time (Roemer et al. 1994). On those islands, within-grid density varied approximately 2-3 foxes/km^2 on 4 grids and approximately 6 foxes/km^2 on 1 grid. In contrast, the range of fox density on San Miguel Island during the recorded decline was 8.4 foxes/km^2 on the Willow Canyon grid, 6.4 foxes/km^2 on the San Miguel Hill grid, and 15.9 foxes/km^2 on the Dry Lakebed grid. Anecdotal information (Laughrin 1980) indicates that island fox populations have fluctuated widely in historic times, for unknown reasons.

The decline on San Miguel Island was not accompanied by declines in adult fox weight, an index of animal condition. Average weights for adult males and females on San Miguel Island (2.25 kg and 2.06 kg, respectively) were higher than those reported for island fox on Santa Cruz Island (2.01 and 1.88 kg) (Crooks 1994). Pup weights declined over time during the study.

Two measures of reproductive effort (number of lactating females, and litter size) decreased during the study period, as density decreased. The number of lactating females was highly correlated with density, and decreased as density decreased. Proportion of lactating females differed by age class, with Age Class 2 and 3 females having a higher proportion of lactating females than Age Class 1. Females reproduced well into maturity, with 7 of 9 Age Class 4 females lactating during this study. In 1994, Age Class 4 females comprised 26% (5/19) of the total number of lactating females, and thus the apparent loss of all Age Class 4 individuals after 1994 affected subsequent reproductive effort and success.

Measures of reproductive success (pup production and recruitment, or the number of young adults) also decreased as density decreased. There was limited evidence of negative density-dependent effects; that is, decrease in density was not associated with increased reproduction or recruitment. However, it is possible that there is a lag time between attaining high population density and the onset of negative density-dependent mechanisms. One measure of reproductive effort (proportion of females that lactated) increased following a decrease in density, but another measure (litter size), did not. Rather, decreases in virtually all measures of reproductive effort and success (number of lactating females, number of pups, and litter size) were associated with decreased density and with decreased number of females. Another suggestion of a negative density-dependent effect was the indication of a limit to pup production. Number of pups appeared to level off at high densities .

On the eastern half of the island (Willow Canyon and San Miguel Hill grids), survival of all age groups was initially high, but declined over the study period. The highest density was recorded on the Dry Lakebed grid in 1994, but survival was low from 1994 to 1995, and apparently no foxes survived from 1995 to 1996 on the Dry Lakebed grid, or from 1996 to 1997. We did not document actual mortality of foxes in our study, and it is possible that foxes not seen in subsequent years may have dispersed from the grids. On the Willow Canyon and San Miguel Hill grids in 1997 we recaptured 5 individuals which had not been captured for 2-4 years previously. However, it is

unlikely that a significant number of foxes not recaptured had dispersed away from the grids, because the proportion of the island sampled by the three grids was high, approximately 25% (see effective trap area estimates in Table 7).

Although 1:1 sex ratios have been reported for other island fox populations, overall sex ratio (pooling adults and pups) in this study favored males. Crooks (1994) reported that male:female ratio for island foxes on Santa Cruz Island was 1:1.21, though this did not differ significantly from 1. Moore and Collins (1995) also reported a 1:1 sex ratio for island fox litters on Santa Cruz Island.

Overall sex ratio (number of males per female) in this study was higher for pups than for adults. Pup sex ratio on the east end differed significantly from parity. This implies that survival of males was less than that of females, but adult survival rates did not differ by sex. Female pup survival varied among years and was associated with female pup weights from the previous year.

Recapture of foxes tagged originally during the design phase of the vertebrate monitoring program extended the known longevity record for island foxes. Previous estimates of longevity for free-ranging island foxes were 4-6 years (Moore and Collins 1995), but several foxes captured during this study were estimated be 7-10 years old.

On San Miguel Island, fox population dynamics may be driven primarily by the fate of females in the population. In this study, recruitment into the population was correlated with pup production from the previous year. Pup production, in turn, was correlated with the number of females and the number of lactating females. Moreover, female pup survival, which will affect recruitment and the number of adult females in the population, seemed to be determined by female pup weights from the previous year.

We did not identify factors influencing pup weights, which, in this study, were not associated with adult female weights, with mouse numbers or with precipitation. Some interannual variation in pup weights may be attributed to slight differences in time of sampling from year to year. Pups gain weight rapidly, and a difference in sampling of 2 to 3 weeks may result in weight differences of 200 to 300 g. Moreover, a single measure of pup weight in summer may reflect developmental constraints more than environmental influences (G. Roemer, pers. comm.).

Changes in Food Availability and Weather

We expected to observe declines in food availability, because such changes drive population dynamics of other fox populations, to varying degrees. Changes in food availability drive fox population dynamics primarily through effects on reproduction and nutritional status. Decline in prey availability can result in fewer females breeding, smaller litters, fewer pups, or lower pup survival to yearling stage. Such effects on reproduction have been observed for fox populations closely linked to single food sources (kit fox (*Vulpes macrotus*): Egoscue 1975, White and Ralls 1993; mainland arctic fox (*Alopex lagopus*): MacPherson 1969; insular red fox (*Vulpes vulpes*): Zabel and Taggart 1989; mainland red fox: Goszczynski 1989), as well as the generalist gray fox (Root and Payne 1985).

In arctic fox, continental populations fluctuate in concert with population cycles of lemmings (*Lemmus groenlandicus* and *Dicrostonyx trimucronatus*), their primary prey (MacPherson 1969). Insular populations of arctic fox fluctuate less, because prey populations vary less, and because foxes have access to other food sources, such as pinniped carrion and seabirds (Hiruki and

Stirling 1989, Fay and Rausch 1992). Density of an insular population of red fox which had access to superabundant food supply (nesting seabirds) was an order of magnitude higher than density reported for mainland populations (Zabel and Taggart 1989). A change in food availability also caused a shift in mating system of that population from polygyny to monogamy.

Kit fox populations also fluctuate according to prey availability (Egoscue 1975, White et al. 1996), perhaps due to the inability or unwillingness of kit foxes to shift to secondary prey species when primary prey species decline. Kit foxes have been shown to maintain relatively exclusive home ranges of sufficient size to sustain their own body mass and conditions during periods of prey scarcity (White and Ralls 1993) as an adaptation to drought-induced periods of prey scarcity that are episodic and temporary in the desert Southwest of the continental United States.

We expected the decline in the fox population be accompanied by declines in food, but this was not the case, at least for the prey items that we monitored. Like the mainland gray fox, the island fox is a generalist omnivore which does not rely on a single prey species (Moore and Collins 1995). Island fox diet changes seasonally according to availability of food items. The most important food items for island foxes on San Miguel Island, deer mice and sea-fig, did not appear to decline over the study period. Deer mice, which were reported to be present in 11-76% of San Miguel Island fox scats (Collins and Laughrin 1979), did not decline over the study period.

Sea-fig has been reported to account for 30-90% volume of fox scats in all seasons (Collins and Laughrin 1979) and was most important in summer. Relative cover of sea-fig did not decline during the study period, although measurement of sea-fig cover may not accurately reflect fruit availability. Additionally, there is a scale-induced

die-off of sea-fig occurring near Simonton Cove which the vegetation monitoring program did not detect in its transects (K. McEachern, pers. comm.).

We did not monitor invertebrate populations, and may have missed seasonal and annual fluctuation in invertebrates. Insects are seasonally important in San Miguel Island fox diets, accounting for 35% and 23% of the total volume of scats in spring and summer, respectively (Collins and Laughrin 1979). It is possible that insect availability may have changed over the study period due to weather, and could have affected fox populations.

Although we expected the fox population decline to be accompanied by changes in food availability and weather, those factors may not vary as much on San Miguel Island as they do on other islands. Ambient temperatures on San Miguel Island are cooler and less variable than on other islands. Johnson (1972) found that San Miguel Island temperatures are cooler than those of mainland and other island stations, and vary less on an annual basis, due to the following factors. First, the cooler ocean temperatures cool the overlying air. Second, the small surface area of San Miguel does not allow for significant diurnal thermal heating. Last, due to the island's low elevations, all the island lies within the cool marine layer that prevailing northwest winds push over the island. Persistent spring and summer fog and low stratus depress temperatures, result in persistently high relative humidities, reduce evapotranspiration, and augment rainfall. The fog patterns at San Miguel are more characteristic of fog patterns of the central California coast, than of the southern California Bight.

Interannual variation in precipitation on the Channel Islands is significant (Fig. 19, Johnson 1979). The rainfall pattern at San Miguel is characterized by periods of drought and periods of heavy precipitation brought about by El Niño

conditions. During the latter, changes in tropical sea surface temperature patterns affect atmospheric circulation patterns (Cane 1983). In southern California and the Southwest, there is an intensification and southward displacement of the normal westerly jet stream, producing an unusual number of winter storms on the California coast. The major El Niño events of 1957-58, 1969, 1972 and 1983 are reflected in the precipitation record for Santa Rosa Island (Fig. 19).

Although interannual variation in precipitation is great, the persistent fog layer on San Miguel Island is an additional source of precipitation that moderates the effects of drought and El Niño conditions. Estberg (1996) measured fog water deposition at San Miguel Island and found that fog water input was equivalent to rainfall input during 1995-1996. Goonetilleke (1996) compared fog deposition at San Miguel Island and at Torrey Pines State Park, and found that San Miguel Island received over twice as much fog water as did the mainland site. The significant contribution of fog water to overall precipitation at San Miguel, compared to the other islands and to the mainland, may serve to dampen the effects of drought years characterized by low annual rainfall. Not only is evapotranspiration less on San Miguel Island, due to low temperatures and high humidities, but fog water lessens the interannual variation in water available to plants and animals. Interannual variation in plant productivity may therefore be less on San Miguel Island, and this may account for lack of fluctuation in San Miguel Island deer mouse populations, compared to other islands.

Deer mouse densities on other Channel Islands vary considerably. During the study period, fall deer mouse densities on Santa Barbara Island varied from <5 mice/ha to over 650 mice/ha (Schwemm 1995, Austin 1995, 1996), whereas deer mouse densities on San Miguel Island varied between 150 and >400 mice/ha. Drost and Fellers (1991) found that deer mouse populations on

Santa Barbara Island increased following winters with high rainfall, and thought that deer mouse population decline may be associated with winters of low rainfall. However, the heavy winter rainfall of 1994-1995 did not appear to increase deer mouse densities on San Miguel Island. Heavy rainfall periods attributed to El Niño conditions have caused rapid increases in rodent populations in other areas (Meserve et al. 1995). The lower interannual variability in deer mouse density on San Miguel Island may result from the lower fluctuation in total precipitation, which includes that derived from fog water deposition. Higher mouse densities on San Miguel, and the high incidence of mice in San Miguel Island fox scats (Collins and Laughrin 1979), may account for the initially high island fox densities recorded during this study. Mice provide significantly higher fat and crude protein than does plant material (Ball and Golightly 1992).

San Miguel Island is subject to periodic drought caused by El Niño - Southern Oscillation events, but it is unknown whether this results in prey scarcity. Periodic drought has had profound effects on San Miguel Island vegetation. Johnson (1979, 1980) studied the existing weather record for San Miguel Island and California and concluded that dry-trend years occurred during 1856-1864, 1869-1883, 1893-1904, 1917-1935, and 1944-64. Periodic drought combined with overgrazing by sheep on San Miguel Island resulted in episodes of massive vegetation stripping and soil erosion that began during the acute droughts of 1863-1865 and 1870. By 1929, these factors had produced an island landscape dominated by shifting sand dunes. Since that time, island vegetation has been slowly expanding.

We began monitoring foxes after a 6 year drought had ceased, and thus cannot quantify the effects of drought on San Miguel Island foxes and their food base. However, record precipitation in 1995 did not result in higher mouse densities and higher fox densities. In fact, fox densities declined

in the 2 years following the record precipitation. Unless changes in insect availability occurred, factors other than food availability and weather may have caused the observed island fox population decline.

It is possible that the high precipitation of winter 1994-1995 adversely affected foxes on San Miguel Island. Precipitation was 3 times higher in winter 1994-1995 than in the other 4 years of the study (Fig. 18), and 1994-1995 was the highest precipitation year on record for Santa Rosa Island (Fig. 19). Adult survival was lower in 1994-95 than in 1993-94, for both the east end and west end of the island (Fig. 12). The high precipitation of 1994-95 was not associated with decreases in other population parameters.

Disease

The observed decline in the San Miguel fox population may be due to a disease agent. The pattern of population decline (from west to east) suggests a disease spreading within the fox population in that same direction. Results from this and previous studies (Garcelon et al. 1988) indicate that island foxes on San Miguel Island have antibodies for canine parvovirus and canine adenovirus. Although exposure to canine adenovirus was high for all years, it is unknown whether this has impacted fox populations. Other free-ranging canids have also shown high seroprevalence to canine adenovirus, and the disease can cause high mortality rates in juveniles, according to Garcelon et al. (1992). Those authors documented high seroprevalence rates (72-97%) for 4 of the 6 island fox populations; Santa Cruz and Santa Catalina showed no antibodies to canine adenovirus. Garcelon et al. concluded that the high seroprevalence indicated that canine adenovirus may be enzootic in the island fox populations (e.g., that the fox population serves as the source of the virus, as opposed to an external source). Female pup survival rates declined over the study period,

and perhaps were influenced by canine adenovirus.

No antibodies to canine distemper have been found in any of the fox populations on the Channel Islands, suggesting that either distemper has never been introduced to island fox populations, or that island foxes are extremely susceptible to distemper and none survived exposure (Garcelon et al. 1992). Canine distemper has been identified as a factor in periodic local population declines of gray foxes on the California mainland (P. Swift, California Department of Fish and Game, pers. comm.) and may have accounted for as much as half of the observed mortality in a gray fox population in Alabama (Nicholson and Hill 1984). On San Miguel Island, occasional visits by domestic dogs could expose island foxes to various diseases. Although domestic dogs are not allowed on the island, boaters have been observed bringing their pets ashore on San Miguel Island (I. Williams, pers. comm.) and on nearby Santa Cruz Island (G. Roemer, pers. comm.).

It is also possible that island foxes on San Miguel may have been exposed to San Miguel sea lion virus (SMSLV), a member of the calicivirus group which commonly crosses species barriers. SMSLV is always present in sea lions (*Zalophus californianus*) and northern fur seals (*Callorhinus ursinus*) on San Miguel, where it causes vesicular lesions on the flippers of pups (R. DeLong, National Marine Fisheries Service, pers. comm.). Thus far it has not been linked to sea lion mortality, but apparently the virus mutates annually, creating new varieties, some of which are more virulent than others. A previous study (Prato et al. 1977) found that both island foxes and feral pigs (*Sus scrofa*) on Santa Cruz Island showed antibodies for SMSLV. It is unknown at this time whether San Miguel foxes have ever been exposed to SMSLV (perhaps from scavenging on pinniped carcasses), or whether exposure to the disease affects fox health. If disease was the agent, the direction of the decline in the San

Miguel Island fox population suggests a disease originating at the west end of the island near Pt. Bennett, the island's largest pinniped rookery.

During the decline, fox carcasses were not collected and necropsied, or examined for clinical evidence of disease. Without such evidence, it is difficult to rule out disease as a factor.

Predation

Predation by golden eagles (*Aquila chrysaetos*) has been identified as contributing to a decline in island fox on a portion of Santa Cruz Island (G. Roemer, unpubl. data). Based on carcass condition, and the presence of golden eagle feathers at 5 carcasses, golden eagles were considered to be the predator in 23 confirmed mortalities on Santa Cruz Island. It is estimated that a single golden eagle could take between 2 and 5 foxes per week (D. Garcelon, pers. comm.). The effect of predation on San Miguel foxes is currently unknown. During the study period, there were only two recorded observations of golden eagles from San Miguel Island. Both observations occurred in 1995. In 1997, a single fox carcass from near the Dry Lakebed grid showed signs of predation by a golden eagle (G. Roemer, pers.comm.). Since few carcasses have been found and examined for such evidence, it is possible that golden eagle predation accounted for some portion of the observed population decline.

Conclusion

During a 5 year study period we observed a considerable population decline of island fox on San Miguel Island. Significant spatial and temporal variation in island fox density on San Miguel Island was not apparently associated with environmental variables, or with prey abundance. Prey (deer mouse) populations did not change significantly

over the study period, and it is likely that they vary less on San Miguel than on other islands, given the relative stability of the weather regime. Sea-fig did not decline over the study period, either. We cannot rule out changes in insect availability as a causative factor, since we did not monitor insects. Effects of predators such as golden eagles are unknown. The relative contribution of canine or other diseases to the observed population decline on San Miguel Island is currently unknown, although canine adenovirus appears to be enzootic in the population.

Changes in island fox population density on San Miguel Island may be driven by survival of female pups and subsequent recruitment of females into the adult population. Only slight negative density-dependent effects were observed in this study, and fox populations may to slow to recover following a catastrophic decline.

Management Recommendations

The observed population decline of island fox on San Miguel Island comprises a "red flag" situation which warrants further investigation of cause and effect relationships. Although the current island fox monitoring program provides a more complete dataset than any other terrestrial protocol at Channel Islands National Park, it is still insufficient to tease out the factors responsible for the observed population decline. Active and in-depth research is required to determine those factors.

We recommend that the Park support or seek funding for the following investigations:

- Determine the role that disease plays in influencing island fox population dynamics on San Miguel Island. This will require periodic serological surveys and examination of fox carcasses for clinical evidence of disease.

- Use radiotelemetry to determine the characteristics of dispersal of pups and causes of pup mortality.

Other investigations are capable of being conducted in-house or with little additional expenditure. These include the current master's thesis investigation of island fox diet and prey availability. We recommend that the Park consider continuing monitoring of prey populations and fox diet after the master's project is completed. A longer term look at food habits and prey availability may be required to establish the full range of variability for these factors. Thus, we need to increase the resolution of the monitoring program at this juncture, at least for island fox, in order to determine the factors that drive fox population dynamics. This will require a sustainable program that includes monitoring of insects and sea-fig availability, regular scat sampling and diet analysis. The Canon Expedition into the Parks grant that we received for 1998-99 should allow us to get a head start on such a sustainable, comprehensive monitoring program.

It is possible that the range of population decline observed in this study period is natural, and does not indicate a management situation requiring mitigation. However, the data reported thus far raise the specter of a local extirpation of island fox on San Miguel Island. Until the factors for the decline are identified, we recommend that the Park consider these data a "red flag" requiring a commitment of staff and funding for its resolution, and, if need be, for its mitigation.

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